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Polar bear foraging behavior during the ice-free period in western Hudson Bay: observations, origins, and potential significance

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ABSTRACT

During much of the year, polar bears in western Hudson Bay use energy-conserving hunting tactics, such as still-hunting and stalking, to capture seals from sea-ice platforms. Such hunting allows these bears to accumulate a majority of the annual fat reserves that sustain them on land through the ice-free season. As climate change has led to earlier spring sea-ice breakup in western Hudson Bay, polar bears have less time to hunt seals, especially seal pups in their spring birthing lairs. Concerns have been raised as to whether this will lead to a shortfall in the bears' annual energy budget. Research based on scat analyses indicates that over the past 40 years at least some of these polar bears eat a variety of food during the ice-free season and are opportunistically taking advantage of a changing and increasing terrestrial prey base. Whether this food will offset anticipated shortfalls and whether land-based foraging will spread throughout the population is not yet known, and full resolution of the issues requires detailed physiological and genetic research. For insight on these issues, we present detailed observations on polar bears hunting without an ice platform. We compare the hunting tactics to those of polar bears using an ice platform and to those of the closely related grizzly bear. We examine how the techniques are related and explore how they may have evolved. We also discuss how they may contribute to polar bear adaptability in the face of climate change projections.

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INTRODUCTION

Polar bears (*Ursus maritimus*) in western Hudson Bay (henceforth WH) primarily hunt ringed seals (*Phoca hispida*) and less frequently bearded seals (*Erignathus barbatus*) and other marine mammals while on the sea ice (Stirling and Archibald, 1977; Thiemann et al., 2008). The most common hunting tactic they use is still-hunting, a type of ambush whereby a polar bear waits by a breathing hole for a seal to emerge before attacking (Stirling, 1974). Polar bears also stalk seals both on the ice and from the water to surprise those hauled out on ice and to attack newborn pups in their birth lairs (e.g., Stirling, 1974; Smith, 1980).

Currently, polar bears rely on these seals as a primary energy source (e.g., Thiemann et al., 2008). In the more southern populations, bears depend on the reserves accumulated from eating pups in the spring to sustain them through the ice-free season, when they are forced onto land for extended periods (Stirling and Derocher, 1993; Stirling, 2011). Climate change is causing the sea ice in Hudson Bay to melt earlier in spring (Gagnon and Gough, 2005; Stroeve et al., 2012), reducing the time polar bears have to hunt on the ice and resulting in their coming ashore with smaller fat reserves (Stirling et al., 1999; Stirling and Parkinson, 2006). Unless polar bears consume supplemental food on land, many are predicted to starve as the ice-free season continues to expand in Hudson Bay (Molnár et al., 2010; Stirling and Derocher, 2012, but see Gormezano and Rockwell, 2015).

While on land, polar bears have access to energetically rich foods including lesser snow geese (*Anser caerulescens caerulescens*) and their eggs as well as caribou (*Rangifer tarandus)* (Gormezano and Rockwell, 2015). Results from scat analyses indicate that at least some polar bears in WH opportunistically and increasingly consume these land-based prey (Gormezano and Rockwell, 2013a, 2013b). Although there are some anecdotal accounts of predation events on land (Brook and Richardson, 2002; Rockwell and Gormezano, 2009; Iles et al., 2013), detailed descriptions of such behaviors are rare. How land-based prey are captured and consumed may affect the net energetic gains of these activities. The mode of capture may also define the skills required to exploit new resources and influence the extent and speed with which the behaviors can spread through the population (Roughgarden, 1972; Estes et al., 2003; Tinker et al., 2009; Gormezano, 2014). This is especially true since individual bears may differ in physical attributes such as size or skills and learning experiences that could differentially limit the utility of some behaviors (Lunn and Stirling, 1985).

For example, extended pursuits can be energetically costly as polar bears generally require more energy for travel than predicted for mammals of their size (Øritsland et al., 1976; Taylor et al., 1970; Fedak and Seeherman, 1979; Hurst et al., 1982a). These costs, however, vary with the size of the bear and the duration of the pursuit (Best, 1982; Hurst et al., 1982b; Gormezano et al., 2016). In addition, polar bears are prone to hyperthermia from sustained activity in warm ambient temperatures and this may differentially limit the duration of a pursuit (Best, 1982; Gormezano et al., 2016). Such constraints may be, in part, why polar bears generally employ more energetically conservative tactics hunting seals on the ice (Hurst et al., 1982a; Stirling, 2011).

In this paper, we present detailed descriptions of polar bears capturing and consuming both terrestrial and marine-based food during the ice-free season in WH. We compare the

behaviors to those polar bears use to obtain prey from ice platforms. We also compare them to foraging behaviors used by the closely related grizzly bear (*Ursus arctos*). We discuss how the behaviors used by polar bears to capture land-based prey may have developed, especially in light of the shared genetic legacy of the two species (e.g., Hailer et al., 2012; Cahill et al., 2013). Finally, we speculate on how the behaviors and their genetic and evolutionary basis may contribute to the polar bears' ability to respond to the rapid changes in their food supply predicted with climate change.

STUDY AREA AND METHODS

Observations of polar foraging were made opportunistically in the more coastal portions of the Churchill and Cape Churchill Peninsula region of northern Manitoba (fig. 1). The bulk of the habitat is coastal tundra comprised of low-lying salt marsh dominated by *Puccinellia phryganodes* and slightly higher coastal beach ridges dominated by *Leymus arenarius*. There are also areas of gravel and rock outcrop. Moving inland from the coastline, there are a series of parallel, relict beach ridges dominated by stands of willow (*Salix* spp.) and *Rhododendron lapponicum* (Gormezano and Rockwell, 2013a). Near the coast (<2 km), the lower habitat between these ridges is supratidal marsh dominated by willow and birch *(Betula glanulosa*) shrub and graminoids such as *Carex aquatilis* and *Dupontia fisheri*. Moving further inland (>2 km) the relict beach ridges are farther apart and the lower intervening land is freshwater marsh dominated by *C. aquatilis* (Ritchie, 1960; Gormezano and Rockwell, 2013a).

Behavioral observations were made primarily by members of the Hudson Bay Project research team (http://research.amnh.org/users/rfr/hbp) but also by local residents of Churchill, Manitoba, Canada. The residents were interviewed by either L.J.G. or R.F.R. and detailed notes were taken since audio/video recording was not used. A written rendition of the notes was prepared as soon after the interviews as possible (appendix). The same approach was taken with field observations made by members of the research team with either L.J.G. or R.F.R. preparing the rendition from field notes and/or interviews. In some cases, multiple renditions of similar behaviors were combined (appendix). The renditions were also annotated with citations of similar foraging behaviors by polar bears at other locations. General behavioral patterns and hunting tactics were extracted from the renditions (Results).

Observations were made during the course of ecological research carried out from 1984 to 2017 for the period from early May to late August. Much of that research focused on colonially nesting snow geese and common eiders (*Somateria mollissima sedentaria*), which may have seasonally, geographically, and faunistically biased the breadth of the observations to some extent. However, observations of predation on snow geese and other species spanned coastal areas from north of Churchill to south of the Broad River (fig. 1), an area that overlaps approximately the central 25%–30% of range of the WH population of polar bears during the ice-free period (cf. Stirling and Derocher, 2012). Most of our ecological work, and hence the observations, occurred during the daytime although trail cameras positioned at snow goose and common eider nests captured some nocturnal behavior beginning in 2012.

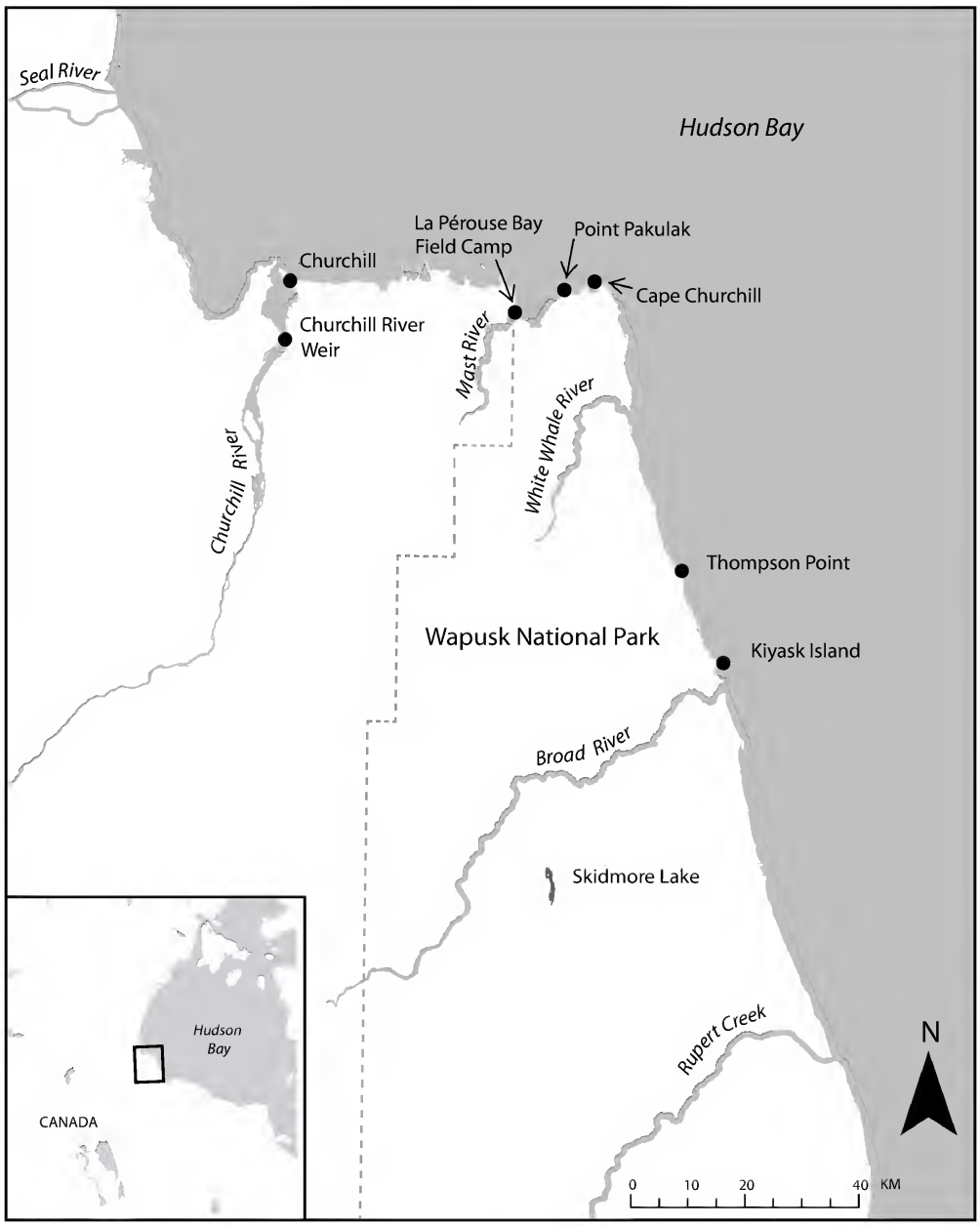

FIGURE 1. Foraging behavior study area with point locations cited in the detailed observations.

RESULTS

We collected behavioral data on polar bears capturing and consuming adults and juveniles of 15 animal species, eggs of three species of water birds and one plant species (table 1 and appendix). Given the opportunistic nature of our data collection, we provide only natural history descriptions of observed behaviors rather than attempt to estimate the relative frequency of these behaviors or to derive any sort of time or activity budgets. Similarly, we cannot conclude that these are the only foraging behaviors and hunting tactics employed by bears in the region. It is worth noting, however, that remains of all the prey items we observed being taken were found in the scat and/or day beds of polar bears distributed from the Seal River to Rupert Creek (fig. 1; Gormezano and Rockwell, 2013a, 2013b). As such, it is likely that the behaviors described are typical for the polar bears of the WH population.

We classified the behaviors and hunting tactics into four categories: chasing, stalking, ambushing, and scavenging.

Chasing. Polar bears throughout the region successfully capture flightless snow geese and their goslings by chasing small flocks into stands of willows and birch that temporarily trap the birds. Before the birds can escape, bears kill several by smashing them with a front paw or biting. Some bears also grab smaller or slower individuals with their mouths during the chase, killing and dropping the bird and, after the chase, returning for it. Bears often chase small flocks of flightless geese into shallow lakes that appear to slow the escape of the geese, allowing the bear to overtake, grab, and kill them. After a long chase or several short chases, bears typically seek shallow streams and lakes and lie down, likely dissipating the heat built up during the pursuit (appendix: 1E; Gormezano et al., 2016). Gormezano et al. (2016) calculated that chases and captures of molting snow geese can be calorically efficient over a range of speeds and distances.

Most chases involve single bears; however, a female and her two yearling cubs were observed working together to corral a small flock of adult and juvenile snow geese against a stand of willows and killing the majority of the birds (appendix: 1A). Numerous common eiders and one northern shoveler (*Anas clypeata*) were chased and caught by single bears after being flushed from nests or while the ducks were performing broken-wing distraction behavior.

Polar bears also chase caribou on the Cape Churchill Peninsula. A bear runs toward a herd and when the caribou scatter, it separates out one individual and attempts to outrun it. Similar chases of small groups were reported by Brook and Richardson (2002) and, like our observations, the chases they observed were not successful (except see appendix: 4C). Rarely, we observed family groups of bears working together trying to outrun and capture lone caribou they had isolated from a group (appendix: 4D).

Stalking. Polar bears stalk female geese and common eiders that are incubating their eggs. The bear gets low to the ground and approaches the bird slowly in a catlike fashion, moving, pausing, and closing the distance to a few meters. It then rushes and grabs the bird with its mouth, crushing it. Miller and Woolridge (1983) reported a willow ptarmigan (*Lagopus lagopus*) captured the same way by a female polar bear in the Churchill area.

Ringed seals (and possibly harbor seals (*Phoca vitulina*), Bajzak et al., 2013) that are near the shore or hauled out onto rocks or sandbars are stalked in a similar fashion. In

TABLE 1. Summary of the prey captured and consumed by polar bears in the Churchill and Cape Churchill Peninsula region. Detailed accounts by prey are given in the appendix.

Prey item	Means of capture	Appendix reference
snow geese	chasing	1A
snow geese	stalking	1B
snow geese	ambush	1C
common eider	chasing	1A
common eider	stalking	1B
other geese and ducks[a]	chasing	1A
other geese and ducks[a]	stalking	1B
tern chicks	scavenging	2
eggs[b]	scavenging	3
caribou	chasing	4C, D
caribou	ambushing	4A
ringed seal	short pursuit	5A
ringed seal	stalking	5C
ringed seal	ambushing	5B
bearded seal	stalking	6
beluga whale	swimming and rushing	7A
beluga whale	ambushing	7B
collared lemming	removing bushes	8
capelin	scavenging	9
northern pike	scavenging	10
lyme grass seed heads	grazing	11

[a] Including Canada geese (*Branta canadensis*), American black duck (*Anas rubripes*), lesser scaup (*Aythya affinis*), northern shoveler (*Anas clypeata*), northern pintail (*Anas acuta*), common eider (*Somateria mollissima*).
[b] Of snow geese, Canada geese, common eider, herring gull (*Larus argentatus*)

some cases the bear prevents the seal from escaping to deeper water with lateral moves. After the bear gets within a few meters it rushes and grabs the seal, usually hauling it above the waterline to kill and consume it (appendix: 5A). Bears walk along the coast in tidal flats near the shore potentially looking for seals hauled out onto the rocks. Remains of seals have been found in polar bear day beds along the coast from Cape Churchill to south of the Broad River, often concentrated in areas of stream outflows that appear to attract seals (R.F.R., personal obs.).

Ambushing. Polar bears ambush snow goose families by lying in shallow streams, such as the Mast River (fig. 1), along indented portions of the bank where higher stands of willow block them from the view of snow goose families walking in the river. As a family passes, the bear charges and often manages to kill one or more individuals with a blow from its paw or by grabbing and crushing with its mouth. The dead geese are usually carried back to the hiding spot and consumed. After eating, the bear waits and charges the next passing family. One of two

bears observed ambushing in this fashion near the La Pérouse Bay Research Station continued feeding this way for nearly two full days (appendix: 1C).

Polar bears use a similar technique to ambush caribou walking along coastal stands of willow and birch. The bear hides behind taller shrubs and waits until the last of a line of caribou passes. It then charges the last animal in line, knocking it over, and then grabbing and biting the animal by the head and neck (appendix: 4A). Ambushing caribou in this manner has been observed south of Cape Churchill near Thomson Point as well as along the western shores of the Churchill River. The technique is also used to ambush seals feeding on fish near the weir in Churchill River. Seals gather at deep pools immediately downstream of the weir and dive for fish that collect there, lounging between feeding bouts. The polar bear hides among the boulders adjacent to the pools and periodically charges, grabs, and kills a seal, and then drags it behind the boulders to eat it (appendix: 5B).

Polar bears also ambush beluga whale calves swimming in the waters at the mouth of the Seal River as the tide goes out. The bear stands on one of the many boulders in the area and leaps onto the back of individuals that swim close to the perch. Often the bear stands waist deep in the water, pressing the dead calf against its chest while eating it from the head downward (appendix: 7B). Ambushing belugas from boulders is no different than ambushing belugas from ice edges and floes (Pedersen, 1962; Perry, 1966; Stirling, 2011).

Scavenging. This includes the acquisition and consumption of sessile forage items that bears encounter walking through various habitats. For example, in multiple years we observed polar bears eating eggs of nesting common eiders, snow geese, and herring gulls (*Larus argentatus*). Bears of all ages and both sexes forage on eggs during both day and night (appendix: 3C). We most frequently observed bears consuming eggs in the 75,000-pair snow goose nesting colony that now spans from just east of Churchill, west to Cape Churchill and south past the Broad River (more than 150 km of coastline; Gormezano and Rockwell, 2015) and in the 300- to 500-nest common eider colony adjacent to the La Pérouse Bay Field Camp (fig. 1). In some cases, an individual bear methodically goes from nest to nest and then island to island in the common eider colony—actually standing on its hind legs to spot the next island. It is less clear whether snow goose nests are located in such a methodical fashion, or whether they are more randomly encountered while bears walk through high-density nesting areas. It is possible that some individual bears know and target these areas for egg scavenging. For example, in 2013 we watched a female with a cub of the year consume a large number of eider nests, and in 2014 we observed a female of similar size with a yearling cub also foraging in the eider colony. Egg scavenging has been observed in several polar bear populations (see citations in appendix: 3D).

A similar "encounter and consume" scavenging approach is observed when bears come upon concentrations of capelin (*Mallotus villosus*) that are trapped in pools among coastal rock formations immediately after the tide goes out. Bears move from pool to pool and consume mouthfuls of the fish (appendix: 9). This has been observed from just east of Churchill to La Pérouse Bay and in the shoals east of the Canadian Wildlife Service tower at Cape Churchill (fig. 1). Northern pike (*Esox lucius*) that are encountered in the flooded *Carex aquatilis* stands that form a 1–2 m border in the shallows along the shore of Skidmore Lake in the center of Wapusk National Park are grabbed, killed, and consumed (appendix: 10).

DISCUSSION

The *ambushing* and *stalking* tactics used to acquire prey during the ice-free period are identical to the behaviors polar bears use to catch seals and other marine mammals from ice platforms (Stirling, 1974; Stirling and Archibald, 1977; Stirling, 2011). For example, hiding and waiting for a herd of caribou or a goose family to pass is no different than still-hunting a seal by waiting by its breathing hole. Stalking a nesting goose or duck is no different than stalking a seal hauled out on the ice (cf. Derocher et al., 2000). All that has changed is the target or, in some cases, the hunting platform. Aside from the burst of speed required for the final attack, relatively little energy would be expended with either of these surprise techniques and the amount would not likely differ when applied in ice-based or ice-free situations. Polar bears are naturally camouflaged on the ice for ambushing and stalking and submerge in seawater during an aquatic stalk of seals hauled out on ice (Stirling, 1974). In contrast, polar bears are conspicuous on terrestrial landscapes in the ice-free season but appear to make use of landscape features to mask their ambushes and stalks during this time, hiding behind vegetation (mainly willow shrubs) and beach ridges and submerging themselves in streams, lakes, and ponds.

The *chasing* technique described here is generally not employed by bears for ice-based hunting, in great part because the majority of polar bears' marine mammal prey are aquatic and do not flee in the same fashion as terrestrial prey. However, polar bears are known to rush for up to 50 m on ice to capture seals (Stirling, 2011). Furthermore, adult polar bears engage in prolonged pursuits of other, smaller bears (especially cubs) on the ice and these periodically end in predation (R.F.R., personal obs.). Most chases of terrestrial prey we observed involved a short burst of running of less than a minute although some lasted longer (e.g., Iles et al., 2013). Polar bears engaging in longer chases could be in the process of learning (Pavlic and Passino, 2011; Iles et al., 2013) or deliberately attempting to tire and separate out vulnerable prey, a technique commonly used by grizzly bears (e.g., Gunther and Renkin, 1990). This is likely an energetically more costly tactic than ambushing or stalking but may be profitable, particularly for smaller bears (Gormezano et al., 2016).

Scavenging during the ice-free period is no different than the scavenging displayed, especially by subadult polar bears, when they encounter abandoned carcasses on the ice (Pedersen, 1962; Perry, 1966; Stirling, 2011). This is certainly a lower energetic technique than chasing and possibly even than stalking, especially since it is often done coincidental to normal movement. The energy efficiency of egg scavenging will depend to a great extent on whether the bear is actively targeting and moving from nest to nest, using either olfactory or visual cues as did the bear eating eider eggs (appendix: 3), or if the bear is simply eating eggs from nests as they are randomly encountered (cf. Dey et al., 2017).

The primary difference between ice-based and ice-free tactics, across all four hunting categories, is simply the target. It is clearly established that WH polar bears have a wide variety of targets during the ice-free season (Gormezano and Rockwell, 2013a, 2013b). These targets span multiple trophic levels and include vegetation, birds, eggs, ungulates, and marine mammals. Consuming food without an ice-based platform is not new, given polar bear foraging accounts reported much earlier in the natural history literature (e.g., Pedersen, 1962; Harrington, 1965; Perry, 1966) and has been documented in other subpopulations (e.g., Smith and

Hill, 1996; Dyck and Romberg, 2007; Drent and Prop, 2008; Smith et al., 2010; Voorhees et al., 2014; Prop et al., 2015; Rogers et al., 2015). It is likely becoming more prevalent in WH because the bears are onshore longer. They also are increasingly overlapping new and increasingly abundant prey species and they may be coming ashore with an energy deficit (Cherry et al., 2013; Gormezano and Rockwell, 2013a, 2013b). Such foraging appears to be increasing at other northern locations as well (Stirling and Derocher, 2012). On the land, just like on the ice, polar bears hunt and eat the more abundant and more prevalent prey (e.g., Thiemann et al., 2008; Tartu et al., 2016). The ability to shift forage targets and obtain them using existing hunting tactics provides polar bears with an overall foraging flexibility that could allow them to make use of new resources in a changing environment. This overall foraging flexibility has been observed in several of the polar bear populations (Derocher et al., 2000; Thieman et al., 2008; Voorhees et al., 2014; Tartu et al., 2016).

Foraging flexibility associated with the use of land-based foods by polar bears will contribute to their energetic and nutritional needs only if bears have the associated digestive flexibility and capacity to process those foods. The feeding trials that have been conducted to date with polar bears (Patton, 1975; Best, 1985; Jansen et al., 2003; Dyck and Morin, 2011) have used only some of the land-based foods the bears are known to consume, but those studies have demonstrated digestive capabilities similar to other bear species. This likely reflects the fact that polar bears have retained the unspecialized gut of bears (Ramsay and Hobson, 1991) and that should allow them to digest a range of food similar to that of their nearest relatives, grizzly and black bears (Krause et al., 2008).

Studies of grizzly and black bears have included a broader range of land-based foods and shown their capacities to efficiently digest and metabolize a variety of both animals and plants (Pritchard and Robbins, 1990; Welch et al., 1997). Unfortunately, no studies of any species of bear have directly assessed the extent to which digestive capability may constrain more rapid diet switching and ultimately diet breadth (Karasov and McWilliams, 2005). Given that the foods typically eaten by polar bears are relatively similar to those of black and grizzly bears in nutritional composition (i.e., high in protein and fat), the consumption of a variety of land-based animals and their products (e.g., eggs) does not likely require substantial changes to the digestive system (Robbins, 1993). However, additional feeding trials involving the many land-based foods polar bears consume should be performed (cf. Dyck and Morin, 2011) and they would aid in evaluating the extent to which digestive constraints may limit the utility of certain land-based foods.

Grizzly bears use similar hunting tactics to obtain many of the same foods consumed by polar bears. For example, grizzlies use ambushing, stalking, and chasing techniques to capture caribou and other ungulates (Gunn and Miller, 1982; Gunther and Renkin, 1990; French and French, 1990; Ovsyanikov, 1996; Young and McCabe, 1998) and are known to scavenge waterfowl eggs and young (Campbell., 1990; Johnson and Noel, 2005; Edwards et al., 2011). They are more often found fishing in faster-moving, shallow rivers and streams, but the techniques they use to capture salmon (*Oncorhynchus spp)* and cutthroat trout (*Oncorhynchus clarkii*) (Luque and Stokes, 1976; Mattson and Reinhart, 1995) are similar to those polar bears use to

capture northern pike (appendix: 10), arctic char (*Salvelinus alpinus*), and four-horned sculpin (*Myoxocephalus quadricornis*) (Dyck and Romberg, 2007).

Like grizzly bears, polar bears sniff out and capture small mammals (Mealey, 1980; appendix: 8) and consume grasses, berries, and other vegetation as part of a mixed diet (Mealey, 1980; Servheen, 1983; Edwards et al., 2011; appendix: 11). Mated pairs and family groups of grizzly bears have been observed hunting elk (*Cervus canadensis*) in what appears to be a cooperative fashion (Cole, 1972; Gunther and Renkin, 1990). Similarly, we observed apparent cooperative hunting between a female polar bear and her two yearling cubs pursuing geese and another female and her yearling cub pursuing caribou (appendix: 1A, 4D).

Both polar and grizzly bears display foraging flexibility, employing similar sets of tactics to acquire a variety of food from a land-based platform. Within a population, such flexibility may reflect either different individuals using specific tactics and targets (specialists) or all individuals using the total range of tactics and targets (generalists). These extremes are the endpoints of a continuum of solutions to the classic niche-width problem posed by Van Valen (1965). This was recently explored in grizzly bears by Edwards et al. (2011) and Van Daele et al. (2012) who showed that while some individuals show some specialization, most are closer to the generalist end of the continuum. Although there have been no formal studies evaluating the width of individual and total feeding niches of polar bears (sensu Bolnick et al., 2003), Stirling (2011) notes that some polar bears specialize in what he calls aquatic stalks of seals. This is, however, a summer activity and those using that technique doubtless switch to other stalking and ambushing tactics in the winter.

We have observed individual polar bears stalking common eiders then switching to chasing snow goose families when the latter suddenly appear. We have also observed bears chasing American black ducks (*Anas rubripes*), and then shifting to stalking a seal that arrived nearby. It is also worth noting that many of the 642 polar bear scats evaluated by Gormezano and Rockwell (2013a) contained more than one (and up to six) food items and that in many cases the combinations would have required using more than one of the hunting tactics observed. It is likely that polar bears, similar to grizzly bears (Edwards et al., 2011; Van Daele et al., 2012), employ a mix of specialist and generalist tactics. Such a mixed strategy would be consistent with conclusions reached by Thieman et al. (2011), whose examination of polar bear diet specialization was limited to marine mammals, and Tartu et al. (2016), who considered both marine and land-based prey.

It is possible that flexible foraging has evolved independently in grizzly and polar bears. It is more likely, however, that the commonalities reflect a shared genetic and evolutionary legacy of the two species (Hailer et al., 2012; Cahill et al., 2013; Weber et al., 2013), even after taking into account that polar bears have developed traits (especially morphological ones) that enable them to exploit an ice-based environment (Stirling, 2011; Rode et al., 2014). While the genetic architecture underlying flexible foraging is not known, it is likely that it depends to some degree on phenotypic behavioral plasticity that shifts depending on the circumstances and targets (e.g., Weaver et al., 1996; Agosta and Klemens, 2008; Geinapp et al., 2007; Gormezano and Rockwell, 2013a). Phenotypic plasticity affords individuals with what Dobzhansky (1970) first described as "adaptability," whereby the expression of a trait originally selected to increase

fitness in one circumstance is altered to increase fitness in another, novel circumstance. This concept has more recently been associated with the notion of a "robust genotype" that contributes to an "ecological fitting," so individuals can successfully exploit novel portions of their environment (e.g., Agosta and Klemens, 2008).

Flexible foraging should allow WH polar bears to more fully exploit newly available and increasingly abundant land-based forage, such as snow geese and caribou on the Cape Churchill Peninsula, and it is firmly established that some individuals are doing just that (Gormezano and Rockwell, 2013a, 2013b). However, it is not known what proportion of individuals in the WH population is currently exploiting the land-based resources, although it is likely that not all bears are doing so (Gormezano and Rockwell, 2013a, 2013b). Onshore arrival of WH polar bears is temporally staggered (Cherry et al., 2013) and no doubt some individuals arrive after certain resources become unavailable (e.g., incubating snow geese, calving caribou). Furthermore, individuals may differ in physical constraints (e.g., size; Brose, 2010), skills, or learning experiences (Lunn and Stirling, 1985), and this could translate into individual variation in choice or capture success of various prey (e.g., Caldow et al., 1999; Estes et al., 2003). Finally, because some of the resources are relatively new, some individuals may currently lack the familiarity or experience to effectively exploit them (Gormezano and Rockwell, 2013a).

If indeed flexible foraging derives from an inherited evolutionary legacy and is based on phenotypic plasticity, then it would equip polar bears with the behavioral tools to rapidly exploit land-based foods without having to evolve new foraging tactics through changes in genetic constitution (Agosta and Klemens, 2008; Gienapp et al., 2008). The use of land-based food could also become increasingly common in the WH population because it is well known that polar bears learn from their mothers, from other bears, and by positive reinforcement of investigative behavior (Stirling, 1974; Lunn and Stirling, 1985; Stirling, 2011; Iles et al., 2013). This should lead to more bears using a wider range of hunting tactics and targets. Although physical adaptations that likely facilitated polar bears' successful expansion in an ice-dominated environment (e.g., Harington, 2008; Stirling, 2011) might impair full implementation of some ancestral land-based foraging strategies (e.g., Ghalambor et al., 2007), the breadth of available hunting tactics may obviate such constraints. For example, limitations on chases related to size and large, heavy limbs can be supplanted by shifting to ambushing.

There is much to be learned before we can predict whether flexible foraging will enhance polar bear persistence in either the short or long term. Among the more pressing issues are the need to establish how many WH bears are using land-based resources and whether this use is expanding. Simultaneously, there is a need to establish the extent of specialization among various demographic classes as has been done with grizzly bears (Edwards et al., 2011). It will also be necessary to move from opportunistically based observations (e.g., this study, Russell, 1975; Smith et al., 2010) to detailed individual studies that will resolve questions on specialization regarding terrestrial foods, and also allow the construction of precise time and energy budgets (Dyck and Kebreab, 2009; Rode et al., 2014). And, finally, we must conduct detailed physiological studies on both captive and free-ranging bears that allow us to estimate both the costs of obtaining land-based prey and their nutritional and energetic value.

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REFERENCES

Abraham, K.F., P. Mineau, and F. Cooke. 1977. Unusual predators of snow goose eggs. Canadian-Field Naturalist 91: 317–318.

Agosta, S.J., and J.A. Klemens. 2008. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecological Letters 11: 1123–1134.

Bajzak, C.E., W. Bernhardt, A. Mosnier, M.O. Hammill, and I. Stirling. 2013. Habitat use by harbor seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. Polar Biology 36: 477–491.

Best, R.C. 1982. Thermoregulation in resting and active polar bears. Journal of Comparative Physiology 146: 63–73.

Best, R.C. 1985. Digestibility of ringed seals by the polar bear. Canadian Journal of Zoology 63: 1033–1036.

Bolnick, D.I., et al. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161: 1–28.

Brook, R.K., and E.S. Richardson. 2002. Observations of polar bear predatory behavior toward caribou. Arctic 55: 193–196.

Brose, U. 2010. Body-mass constraints on foraging behaviour determine population and food-web dynamics. Functional Ecology 24: 28–34.

Cahill, J.A., et al. 2013. Genomic evidence for island population conversion resolves conflicting theories of polar bear evolution. PLOS Genetics 9 (3): e1003345. [doi: 10.1371/journal.pgen.1003345]

Caldow, R.W.G., et al. 1999. Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. Journal of Animal Ecology 68: 869–878.

Campbell, B.H. 1990. Factors affecting the nesting success of Dusky Canada Geese, *Branta Canadensis occidentalis,* on the Copper River Delta, Alaska. Canadian Field-Naturalist 104: 567–574.

Cherry, S.G., A.E. Derocher, G.W. Thiemann, and N.J. Lunn. 2013. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. Journal of Animal Ecology 82: 912–921.

Cole, G.F. 1972. Grizzly bear-elk relationships in Yellowstone National Park. Journal of Wildlife Management 36: 556–561.

Derocher A.E., Ø. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. Polar Biology 23: 675–678.

Dey, C., et al. 2017. Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea ice loss. Global Change Biology 23: 1821–1831.

Dobzhansky, T. 1970. Genetics of the evolutionary process. New York: Columbia University Press, 505 pp.

Drent, R., and J. Prop. 2008. Barnacle goose (*Branta leucopsis*) surveys on Nordenskiöldkysten, west Spitzbergen 1975–2007; breeding in relation to carrying capacity and predator impact. Circumpolar Studies 4: 59–83.

Dyck, M., and E. Kebreab. 2009. Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget. Journal of Mammalogy 90 (3): 585–593.

Dyck, M.G., and P. Morin. 2011. In vivo digestibility trials of a captive polat bear (*Ursus maritimus*) feeding on harp seal (*Pagophilus groenlandicus*) and arctic char (*Salvelinus alpinus*). Pakistan Journal of Zoology 43: 759–767.

Dyck, M.G., and S. Romberg. 2007. Observations of a wild polar bear (*Ursus maritimus*) successfully fishing arctic charr (*Salvelinus alpinus*) and fourhorn sculpin (*Myoxocephalus quadricornis*). Polar Biology 30: 1625–1628.

Edwards, M.A., A.E. Derocher, K.A. Hobson, M. Branigan, and J.A. Nagy. 2011. Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. Oecologia 165: 877–889.

Estes, J.A., M.L. Riedman, M.M. Staedler, M.T. Tinker, and B.E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. Journal of Animal Ecology 72: 144–155.

Fedak, M.A., and H.J. Seeherman. 1979. Re-appraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. Nature 282: 713–716.

French, S.P., and M.G. French. 1990. Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986–88. Bears: Their Biology and Management 8: 335–341.

Furnell, D.J., and D. Oolooyuk. 1980. Polar bear predation on ringed seals in ice free water. Canadian Field-Naturalist 94: 88–89.

Gagnon, A.S., and W.A. Gough. 2005. Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. Arctic 58: 370–382.

Geinapp, P, C. Teplitsky, J.S. Alho, J.A., Mills, and J. Merila. 2007. Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17: 167–178.

Ghalambor, C.K., J.K. McKay, S.P. Carroll, and D.N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21: 394–407.

Gormezano, L.J. 2014. How important is land-based foraging to polar bears (*Ursus maritimus*) during the ice-free season in western Hudson Bay? An examination of dietary shifts, compositional patterns, behavioral observations and energetic contributions. Ph.D. dissertation, City University of New York, New York.

Gormezano, L.J., and R.F. Rockwell. 2013a. What to eat now? Shifts in polar bear diet during the ice-free season in western Hudson Bay. Ecology and Evolution Ecology and Evolution 3 (10): 3509–3523.

Gormezano, L.J., and R.F. Rockwell. 2013b. Dietary composition and spatial patterns of polar bear foraging on land in western Hudson Bay. BMC Ecology 13: 51–64. [doi: 10.1186/1472-6785-13-51]

Gormezano, L.J., and R.F. Rockwell. 2015. The energetic value of land-based foods in western Hudson Bay and their potential to alleviate energy deficits of starving adult male polar bears. PLOS One. [doi: 10.1371/journal.pone.0128520]

Gormezano, L.J., S.R. McWilliams, D.T. Iles, and R.F. Rockwell. 2016. Costs of locomotion in polar bears: when do the costs outweigh the benefits of chasing down terrestrial prey? Conservation Physiology 4 (1): cow45. [doi: 10.1093/conphys/cow045]

Gunn, A., and F.L. Miller. 1982. Muskox bull killed by a barren-ground grizzly bear, Thelon Game Sanctuary, N.W.T. Arctic 35: 545–546.

Gunther, K.A., and R.A. Renkin. 1990. Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. Bears: Their Biology and Management 8: 329–334.

Hailer, H., et al. 2012. Nuclear genomic sequences reveal that polar bears are an old and distinct bear lineage. Science 336: 344–347.

Harington, C.R. 2008. The evolution of Arctic marine mammals. Ecological Applications 18: S23–S40.

Harrington, C.R. 1965. The life and status of the polar bear. Oryx 8: 169–176.

Heyland, J.D., and K. Hay. 1976. An attack by a polar bear on a juvenile beluga. Arctic 29: 56–57.

Hurst, R.J., M.L. Leonard, P.D. Watts, P. Beckerton, and N.A. Øritsland. 1982a. Polar bear locomotion: body temperature and energetic cost. Canadian Journal of Zoology 60: 40–44.

Hurst, R.J., N.A. Øritsland, and P.D. Watts. 1982b. Body mass, temperature and cost of walking in polar bears. Acta Physiologica Scandinavia 115: 391–395.

Iles, D.T., S.L. Peterson, L.J. Gormezano, D.N. Koons, and R.F. Rockwell. 2013. Terrestrial predation by polar bears: not just a wild goose chase. Polar Biology 36: 1373–1379.

Jansen W.A., J.B. Rhenen, E.J.B. Veldhuis Kroeze, A. Wellen, and A.C. Beynen. 2003. Apparent digestibility of macro-nutrients in captive polar bears (*Ursus maritimus*). Zoological Garten 2: 111–115.

Johnson, S.R., and L.E. Noel. 2005. Temperature and predation effects on abundance and distribution of Lesser Snow Geese on the Sagavanirktok River Delta, Alaska. Waterbirds 28: 292–300.

Karasov W.H., and S.R. McWilliams. 2005. Digestive constraints in mammalian and avian ecology. *In* J.M. Stark and T. Wang (editors), Physiological and ecological constraints to feeding in vertebrates. Enfield, NH: Science Publishers.

Krause, J., et al. 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evolutionary Biology 8: 220.

Lunn, N.J., and I. Stirling. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. Canadian Journal of Zoology 63: 2291–2297.

Luque, M.H., and A.W. Stokes. 1976. Fishing behaviour of Alaskan brown bear. Bears: Their Biology and Management 3: 71–78.

Madsen, J., T. Bregnballe, J. Frikke, and I.B. Kristensen. 1998. Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard Light-bellied Brent Geese *Branta bernicla hrota*. Norsk Polarinstitutt Skrifter 200: 221–234.

Mattson, D.J., and D.P. Reinhart. 1995. Influence of cutthroat trout (*Oncorhynchus clarki*) on behavior and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. Canadian Journal of Zoology 73: 2072–2079.

Mealey, S.P. 1980. The natural food habits of grizzly bears in Yellowstone National Park, 1973–74. Bears: Their Biology and Management 4: 281–292.

Miller, G.D., and D.R. Woolridge. 1983. Small game hunting behaviour of polar bears, *Ursus maritimus*. Canadian Field-Naturalist 97: 93–94.

Molnár, P.K., A.E. Derocher, G.W. Thiemann, and M.A. Lewis. 2010. Predicting survival, reproduction and abundance of polar bears under climate change. Biological Conservation 143: 1612–1622.

Øritsland, N.A., C. Jonkel, and K. Ronald. 1976. A respiration chamber for exercising polar bears. Norwegian Journal of Zoology 24: 65–67.

Ovsyanikov, N. 1996. Polar bears – living with the white bear. Stillwater, MN: Voyageur Press.

Patton, R.S. 1975. Digestibility studies on polar bears with emphasis on carbohydrates. American Association of Zoological Parks and Aquaria, Proceedings of the Annual Meeting: 158–161.

Pavlic, T.P., and K.M. Passino. 2011. The sunk-cost effect as an optimal rate-maximizing behavior. Acta Biotheoretica 59: 53–66.

Pedersen, A. 1962. Polar animals. London: Harrap.
Perry, R. 1966. The world of the polar bear. London: Cassell.
Pritchard, G.T., and C.T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68: 1645–1651.
Prop J., et al. 2015. Climate change and the increasing impact of polar bears on bird populations. Frontiers in Ecology and Evolution 3: 1–12.
Ramsay, M.A., and K.A. Hobson. 1991. Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. Oecologia 86: 598–600.
Ritchie, J.C. 1960. The vegetation of northern Manitoba. V. Establishing the major zonation. Arctic 13: 210–229.
Robbins C.T. 1993. Wildlife feeding and nutrition (2nd ed.). Academic Press, New York, NY.
Rockwell, R.F., and L.J. Gormezano. 2009. The early bear gets the goose: climate change, polar bears and lesser snow geese in western Hudson Bay. Polar Biology 32, 539–547.
Rode, K.D, C.T. Robbins, L. Nelson, and S.C. Amstrup. 2014. Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? Frontiers in Ecology and the Environment 13 (3): 138–145.
Rogers, M.C., E. Peacock, K. Simac, M.B. O'Dell, and J.M. Welker. 2015. Diet of female polar bears in the southern Beaufort Sea of Alaska: evidence for an emerging alternative foraging strategy in response to environmental change. Polar Biology 38: 1035–1047.
Roughgarden, J. 1972. Evolution of niche width. American Naturalist 106: 683–718.
Russell, R.H. 1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic 28: 117–129.
Servheen, C. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. Journal of Wildlife Management 47: 1026–1035.
Smith, A.E., and M.R.J. Hill. 1996. Polar bear, *Ursus maritimus*, depredation of Canada Goose, *Branta canadensis*, nests. Canadian Field Naturalist 110: 339–340.
Smith, P.A., K.H. Elliott, A.J. Gaston, and H.G. Gilchrist. 2010. Has early ice clearance increased predation on breeding birds by polar bears? Polar Biology 33: 1149–1153.
Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology 58: 2201–2209.
Smith, T.G. 1985. Polar bears (*Ursus maritimus*) as predators of belugas (*Delphinapterus leucas*). Canadian Field Naturalist 99: 71–75.
Stempniewicz, L. 1993. The polar bear *Ursus maritimus* feeding in a seabird colony in Frans Josef Land. Polar Research 12: 33–36.
Stirling, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Canadian Journal of Zoology 52: 1191–1198.
Stirling, I. 2011. Polar bears: the natural history of a threatened species. Markham, Ontario: Fitzhenry & Whiteside, 300 pp.
Stirling, I., and W.R. Archibald. 1977. Aspects of predation of seals by polar bears. Journal of Fisheries Research Board Canada 34: 1126–1129.
Stirling, I., and A.E. Derocher. 1993. Possible impacts of climatic warming on polar bears. Arctic 46: 240–245.
Stirling, I., and A.E. Derocher. 2012. Effects of climate warming on polar bears: a review of the evidence. Global Change Biology, 18: 2694–2706.
Stirling, I., and C.L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic 59: 261–275.

Stirling, I., N.J. Lunn, and J. Iacozza. 1999. Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climate change. Arctic 52: 294–306.

Stroeve, J.C., et al. 2012. The Arctic's rapidly shrinking sea ice cover: a research synthesis. Climatic Change 110: 1005–1027.

Tartu, S., et al. 2016. Geographical area and life history traits influence diet in an arctic marine predator. PLOS One. [doi: 10.1371/journalpone.155980]

Taylor C.R., K. Schmidt-Nielsen, and J.L. Raab. 1970. Scaling energetic cost of running to body weight of animals. American Journal of Physiology 219: 1104–1107.

Thiemann, G.W., S.J. Iverson, and I. Stirling. 2008. Polar bear diets and arctic marine food webs: insights from fatty acid analysis. Ecological Monographs 78: 591–613.

Thiemann, G.W., S.J. Iverson, I. Stirling, and M.E. Obbard. 2011. Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. Oikos 120: 1469–1478.

Tinker, M.T., M. Mangel, and J.A. Estes. 2009. Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations. Evolutionary Ecology Research 11: 841–869.

Van Daele, L.J., V.G. Barnes, and J.L. Belant. 2012. Ecological flexibility of brown bears on Kodiak Island, Alaska. Ursus 23: 21–29.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99: 377–390.

Voorhees, H., R. Sparks, H.P. Huntington, and K.D. Rode. 2014. Traditional knowledge about polar bears (*Ursus maritimus*) in northwestern Alaska. Arctic 67: 523–536.

Weaver, J.L., P.C. Paquet, and L.F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10: 964–976.

Weber, D.S., et al. 2013. Low MHC variation in the polar bear: implications in the face of Arctic warming? Animal Conservation. [doi: 10.1111/acv.12045]

Welch, C.A., J. Keay, K.C. Kendall, and C.T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78: 1105–1119.

Young, D.D., and T.R. McCabe. 1998. Grizzly bears and calving caribou: what is the relation with river corridors? Journal of Wildlife Management 62: 255–261.

APPENDIX

Detailed Observations of Foraging Behavior

1. Waterfowl

Polar bears regularly catch and consume adults and juveniles of several species of migratory waterfowl including lesser snow geese (*Anser caerulescens caerulescens*, henceforth snow geese), Canada geese (*Branta canadensis*), American black duck (*Anas rubripes*), lesser scaup (*Aythya affinis*), northern shoveler (*Anas clypeata*), northern pintail (*Anas acuta*), and common eider (*Somateria mollissima*). Snow geese and common eiders have been the primary observed prey likely reflecting in part the fact that both are concentrated in nesting colonies. Additionally, snow geese are extremely and increasingly abundant. The bears use three somewhat different strategies to catch adult and juvenile birds: *chasing*, *stalking*, and *ambushing*.

A. Chasing. During the brood-rearing period for snow geese, when neither adults nor goslings can fly, polar bears routinely chase geese in the tidal and supratidal marsh areas around the La Pérouse Bay Research Station and other portions of the Cape Churchill Peninsula, especially where there are shrubs. Bears appear to take advantage of stands of willow and birch that serve as backstops, slowing the flightless geese and reducing their chances for escape (Iles et al., 2013). Once a bear has one goose or more "trapped" against the willows, it generally kills it (them) with a blow from a front paw or by grabbing the goose in its mouth and crushing it. Periodically, bears will grab goslings while chasing a group of geese, kill and drop them, and then return and eat them after the chase. Most pursuits involve a single polar bear; however, R.F.R. and D.T. Koons observed a female and two yearling cubs on 21 July 2008 working together to chase a small flock of adult and juvenile snow geese into a stand of willows and killing a number of the birds. Numerous common eiders and one northern shoveler were chased and caught by single bears after being (inadvertently?) flushed from nests and often while the ducks were performing broken-wing distraction behavior. Chases of geese often involve running the prey into lakes or streams (below). Gormezano et al (2016) calculated that chases and captures of molting snow geese can be calorically efficient over a range of speeds and distances.

B. Stalking. On several occasions in the common eider colony adjacent to the La Pérouse Bay camp and on one observed occasion with a Canada goose and one with a snow goose, a lone polar bear was observed stalking a female that was sitting on her nest. The bear proceeded in a catlike fashion with numerous stops and starts until the distance between it and the nest was only a few meters. The bear then rushed the nest and grabbed the female with its mouth, crushing it. Miller and Woolridge (1983) report a willow ptarmigan (*Lagopus lagopus*) captured the same way by a female polar bear in the Churchill area and B. Knudsen (personal commun., in Russell, 1975) observed two successful stalking attacks on nesting female Canada geese.

C. Ambushing. On two occasions, different polar bears were observed lying in the Mast River along an indented portion of the bank where high stands of willow block them from the view of snow goose families walking in the river. As a family passed, the bear charged the family and often killed one or more gosling with a blow from its front paw or by grabbing and crushing with its mouth.

FIGURE 2. Remains of an adult white-phase lesser snow goose. Typically, the breast, legs, thighs, gizzard, heart, and liver are consumed. In this individual some of the liver remains (29 July 2013).

The gosling(s) was (were) carried back to the hiding spot and consumed. After eating, the bear again waited and charged the next passing family. One of the two bears observed ambushing in this fashion continued it for nearly two full days successfully capturing goslings from at least 20 families.

D. After capturing and killing one or more birds, the bear almost always sits and eats, often slowly. Examining carcasses immediately after the bear leaves, we found that the bears usually consume the breast, thigh, and leg muscles as well as the gizzard and liver. In some cases, the intestines are also consumed (fig. 2). Estimates of the nutritional and energetic value of the geese can be found in Gormezano and Rockwell (2015) and Gormezano et al. (2016).

E. Especially after chasing and capturing several geese, bears were frequently observed moving to ponds or creeks and lying in the water, possibly to cool off (fig. 3; Gormezano et al., 2016). We have also observed them drinking after eating and apparently cleaning fur around their muzzle (cf. Stirling, 2011). In Svalbard, after feeding on multiple barnacle goose (*Branta leucopsis*) eggs and goslings, Drent and Prop (2008) observed polar bears immediately traveled to the mainland to drink from a fresh water pool.

FIGURE 3. After chasing, capturing, and consuming at least three snow geese, this subadult polar bear submerged and lounged in the Mast River on 13 August 2013.

2. Terns

On July 26, 2016, A. Barnas, S.N. and C.J. Felege, and R.F.R. observed a lone subadult male polar bear walking along a sand bar near Cape Churchill. The bear periodically sped up, stopped, leaned down, and appeared to grab something. Closer inspection with a spotting scope revealed the bear was catching and eating flightless arctic tern (*Sterna paradisaea*) chicks. Large numbers of arctic terns nest on the sand and gravel bars in this area and flightless chicks wander about waiting for parents to bring them fish. Revisiting the sand bar a week later, we found several piles of polar bear scat, one of which contained the intact foot of an arctic tern chick.

3. Eggs

A. On 15 July 2003, a single, large polar bear entered the common eider colony adjacent to the La Pérouse Bay Research Station. During the next approximately 96 hours, the bear predated 206 of 325 nests that were being actively incubated. (Had the bear not been chased away by helicopter ~96 hours later for safety reasons, the depredation may have continued.) P.Z. Matulonis and R.F.R. both observed the bear from roofs of the research station buildings with binoculars and spotting scopes. The bear walked from island to island in the nesting colony often stalking, flushing, and chasing incubating females, as described above. Once on the island the bear went from nest to nest and appeared to consume many of the eggs they contained. We visited the nests after the bear had left and found that in most cases all the eggs were gone. In some cases one or two of the eggs appeared to have been crushed and the contents consumed, perhaps in the fashion described by Drent and Prop (2008).

B. A female and cub of the year were observed eating eggs from many eider nests during late June and early July 2013 (fig. 4) and a female with a yearling cub foraged on eider eggs during the same time period in 2014. Because they were not marked, we cannot definitively conclude they were the same bears, although such returns have been described for Svalbard (J. Prop, personal commun.).

FIGURE 4. **A.** This is one of many eider eggs this female polar bear consumed from 25 June to 6 July 2013. **B.** Her cub is seen chewing on remains of the predated nest bowl.

C. Since 2000, there have been numerous observations of polar bears on the snow goose nesting colony during the incubation period. On several occasions bears have been seen through binoculars consuming eggs. Later inspection of the nests revealed egg predation even when actual foraging was not observed. Beginning in 2012, we deployed trail cameras at snow goose and eider nests and inspection of the imagery revealed numerous cases of egg predation by mothers with cubs of the year, mothers with yearlings, subadults, and even one large, obese male. These images revealed that egg predation happens at night as well as during the day (fig. 5).

FIGURE 5. Polar bear eating eider eggs at 03:45 on 19 July 2016.

D. Other examples of polar bear egg foraging include: snow geese in western Hudson Bay (Abraham et al., 1977; Rockwell and Gormezano 2009) and Coats island, Nunavut (Smith et al., 2010), Canada geese on Akimiski Island, Nunavut (Smith and Hill, 1996), little auks (*Alle alle*) on Hooker Island in Frans Josef Land (Stempniewicz, 1993), thick-billed murres on Coats Island (Smith et al., 2010), barnacle geese (Drent and Prop, 2008) and light-bellied brent geese (*Branta bernicla hrota*) in Svalbard, Norway (Madsen et al., 1998).

4. Caribou (*Rangifer tarandus*)

A. At about 11:00 on 17 July 1994, S. Miller (pilot) and R.F.R. were flying south from Cape Churchill in a Bell Jet Ranger helicopter at approximately 200 ft when they observed a polar bear at the south end of a beach ridge near a cabin north of Thompson Point. The bear was sitting on the inland side of a clump of 1–2 m tall willows. We had made a series of slow turns, climbing to about 500 ft when we saw 15 to 20 caribou walking south on the coastal side of the beach ridge. As the caribou passed the end of the beach ridge, the bear charged the end of the line and knocked the trailing caribou to the ground. The bear immediately pounced on the caribou and bit it around the head and neck. We left the area to avoid any further disturbance. We returned to the site at about 12:30 and found the bear and the partially consumed carcass of the caribou near the spot where the attack occurred. The caribou was fairly small, likely a young of the year. M. Macri reported similar ambush attempts and successes on caribou by polar bears. Brook and Richardson (2002) report several cases of polar bears stalking caribou on the Cape Churchill Peninsula.

B. At approximately 09:00 on 6 August 1998, R.F.R. was in a 5 m observation tower located on the shoreline near the base of La Pérouse Bay. He observed a female polar bear, accompanied by one cub of the year, dragging the carcass of a freshly killed caribou calf toward the tower from

FIGURE 6. Remains of a caribou calf in a day bed on Point Pakulak (28 July 2007).

the south along the willow fringe (cf. Derocher et al., 2000). The bears stopped approximately 300 m south southeast of the tower and began eating the calf. The female ripped open the abdominal cavity and she and the cub fed on the thoracic and some abdominal organs. After about 2 hours, the bears retreated about 25 m into 2–3 m tall willows and bedded down. The cub appeared to remain asleep while the female periodically raised her head, looking in the direction of the carcass. At about 12:00, a large, male polar bear approached the carcass from the north and proceeded to feed on the left rear rump and leg. The sow increased the frequency of head raises and eventually sat upright. After about 10 minutes, the cub retreated approximately 25 m inland. The male continued foraging. After another 10–15 minutes, the female charged at the male while vocalizing loudly. The male retreated north about 200 m and sat and watched as the female approached the carcass and dragged it back toward the bed she and the cub had occupied. The male slowly moved north and east across La Pérouse Bay. The female and cub remained in the area for another 2–3 days, feeding on the remains of the carcass.

C. At approximately 11:00 on 28 July 2007, L.J. Gormezano, R.F.R., and C.R. Witte were searching for polar bear scat on Point Pakulak, near Cape Churchill. They noticed a herd of approximately 500 caribou nearby that was moving along the tidal flats in a swirling and undulating fashion. As they watched for nearly 45 minutes, they saw that the herd was being moved by a single, large polar bear. The herd would move slowly away as the bear walked toward them, but as the bear got closer and began running one or two caribou would break away and become isolated from the herd. The bear would chase these individuals, but they would outpace the bear, circle, and rejoin the herd. While we did not see this bear capture a caribou, it is worth noting that there was a polar bear day bed on Point Pakulak that contained the remains of a recently consumed caribou calf (fig. 6). These chasing observations are similar to those reported by Brook and Richardson (2002).

D. On 11 July 2009, R.F.R. observed a female and yearling cub working together in attempts to isolate individual caribou from a small herd. As noted above, the bears chased the herd and

FIGURE 7. Polar bear consuming a recently killed caribou calf on a sand spit near the Broad River on 26 July 2010.

when one or two individual caribou became separated from the herd, the yearling bear chased them while the female tried to get between the individual(s) and the herd. During approximately 60 minutes of observations, the bears were not successful.

E. On 26 July 2010, R.F.R., L. Aubry and K. Uvino observed an adult polar bear consuming a small caribou on a sand spit near the Broad River. Blood on the carcass, the bear and the ground were consistent with the bear having recently killed the caribou. During this time of year, large groups of caribou, including the calves of the year, gather on the coast and in the tidewater to escape insects. Large numbers of polar bears frequent the area during the same time period (fig. 7).

F. On 8 August 2012, R.F.R. and K. Uvino observed 4 adult male polar bears and the remains of a bull caribou on Kiyask Island north of the Broad River in Wapusk National Park. The bears were either standing or lying near each other and each was consuming some of the remains (fig. 8).

5. Ringed Seal (*Phoca hispida*)

A. At 12:20 on 1 August 2008, R.F.R. watched a single polar bear chasing after flightless American black ducks that were foraging in shallow (<0.5 m) tidewater near a gravel spit on the east side of Bird Cove, located approximately 15 km east of Churchill, Manitoba. The bear shifted its attention to what turned out to be a ringed seal swimming in shallow water near the spit about 100 m from the bear. The bear moved toward the seal that, in turn, tried to get to

FIGURE 8. Four adult polar bears eating the remains of a bull caribou on Kiyask Island, 8 August 2012.

the open, deeper water of the outgoing tide. The bear cut the seal off and in about 5 minutes of maneuvering managed to keep the seal between itself and the shore and close the distance between them to about 10 m. The bear began stalking closer and finally rushed and grabbed the seal by the head. It dragged the seal onto the spit and slapped the carcass to the ground several times while still holding it by the head. The bear then sat and consumed much of the seal. Unlike the deeper water seal capture reported by Furnell and Oolooyuk (1980), this polar bear took advantage of shallow water produced by an outgoing tide.

B. Breaches in the weir across the Churchill River, 10 km upstream from Churchill, Manitoba, are caused by ice movements in the spring and the water flowing through them forms deep pools immediately downstream. Ringed seals (and possibly harbor seals (*Phoca vitulina*; Bajzak et al., 2013) gather at these pools, grabbing fish that come through the breaches and catching fish that gather in the deeper water pools. The seals also bask in the sun on nearby boulders. During late July to mid-August of 2008, M. Walkoski was using a heavy front-end loader to place large boulders and riprap in breaches in the weir. Around the first of August, a large polar bear moved into the area and would sit on the boulders or lie in the shallower water during the heat of the day. The seals appeared either to not notice the bear at such times or ignored it. On at least five occasions, the polar bear rushed the basking seals, grabbed one of them by the head, dragged it higher onto the weir, and consumed much of it. Walkoski specifically used ringed seal in his account and not "ranger seal" which is the local name for the harbor seal.

C. On 14 August 2010, R.F.R. and L.J.G. observed a polar bear eating a seal on a gravel spit near the Seal River. The kill was fresh and the bear had blood on its fur. The bear had consumed

FIGURE 9. Polar bear eating the remains of a seal on a gravel spit near the Seal River, 14 August 2010.

the skin and subcutaneous fat. Although this prevented certain identification, ringed seals are common in this area, often basking on gravel spits and feeding on fish at the mouth of the river (fig. 9). R.F.R. and L.J.G. observed several cases where polar bears appeared to patrol the shoreline and stalk seals that were hauled out along areas of braided rivers. The stalking behavior is similar to that described above for birds and is likely how the seal being consumed at the Seal River was obtained. Remains of seals are regularly found in coastal day beds of polar bears (R.F.R., personal obs.).

6. Bearded Seal (*Erignathus barbatus*)

Flying south from Cape Churchill at approximately 10:00 on 18 July 2001 in a Bell 206 Jet Ranger helicopter, J. McRae (pilot) and R.F.R spotted three adult polar bears on a sand and gravel bar south of the northernmost channel of the White Whale River. Closer inspection showed the bears were feeding on the reasonably intact carcass of a recently killed bearded seal. The carcass was approximately 5 m inland and the surrounding gravel was stained with bright red blood, suggesting that the seal had been recently killed. Only a few strips of skin had been pulled off the exposed ventral surface. The abdominal cavity had not been breached. Two of the polar bears had bright red bloodstains around their muzzles and one also had a fresh blood stain high on its chest. We returned to the site at approximately 17:00 and the carcass was partially consumed. Much of the skin on the ventral surface had been stripped away and subcutaneous fat removed. The abdominal and chest cavities had been opened and it appeared that most of the thoracic organs had been consumed. Portions of intestine were scattered about the site. Large portions of dorsal surface of the seal had also been ripped off. All three bears were

resting in lyme grass (*L. arenarius*) day beds nearby and the faces of all three were stained dark red. It is likely this seal had been hauled out on the shore and was stalked and captured. Remains of bearded seals are found periodically in coastal day beds of polar bears.

7. Beluga Whales (*Delphinapterus leucas*)

A. On 4 August 2000, J. McRae (pilot) and R.F.R. observed two polar bears swimming in the Churchill River approximately 0.5 km south of the landing dock for Prince of Wales Fort. We were flying above the river in a Bell Jet Ranger helicopter at approximately 100–150 feet and remained in the area in hovers and slow turns for about 20 minutes. During that time the bears singly and jointly pursued both adult and calf beluga whales. On several occasions one or both of the bears would float with the outgoing tide and as a whale approached the bear(s) would rush it. On other occasions, one or both of the bears would rush laterally at a whale swimming past them. There were also instances of the bears swimming after retreating (fleeing?) whales. We did not see any contact made with the whales. The two polar bears rested near each other on the shore and were seen pursuing beluga whales in the same fashion for at least three more days. M. Macri also observed polar bears floating in the Churchill River and attempting to ambush beluga whales. The pursuits observed were similar to those reported by Heyland and Hay (1976) in Lancaster Sound and Smith (1985) in Cunningham Inlet except those occurred in deeper water.

B. On 12 August 2014, helicopter pilot E. Polzin was ferrying passengers from Churchill, Manitoba, to a lodge north of the Seal River. He observed an adult polar bear standing on one of the many boulders in the mouth of the Seal River. There were numerous beluga whale adults and calves swimming in the outgoing tidewater. The bear was still on the boulder on the return flight to Churchill 15 minutes later and on the second trip to the lodge 30 minutes after that. On his second return flight to Churchill, he saw that the bear was standing about waist deep in the water grasping a beluga calf with his front legs and eating the anterior portion of the now dead calf. It appeared that the bear had leapt from the boulder to capture the whale. Similar observations have been made since 2014 by other helicopter pilots and fishermen in the Churchill area. In 2017, tour guides for Churchill Wild reported at least four large male polar bears killing beluga calves in this fashion north of the Seal River. The behavior seems identical to descriptions of polar bears jumping onto beluga calves from ice edges (Pedersen, 1962; Perry, 1966; Stirling, 2011).

C. The remains of beluga whale calves are periodically found in the day beds of polar bears along the coast (fig. 10).

8. Collared Lemming (*Dicrostonyx richardsoni*)

During observations of goose foraging made from a tower near the high-tide line on the east coast of La Pérouse Bay in July 1985 and 1986, L.C. Newell and R.F.R. observed several different large male polar bears displaying a curious behavior involving willow bushes inland from the tower and what appeared to be collared lemmings. The polar bears moved inland

FIGURE 10. Remains of a beluga whale calf in the day bed of a polar bear that had just left on August 11, 2015.

past the tower and appeared to be sniffing about the bases of the 1–2 m tall willows that formed the interior extent of the coastal snow goose nesting habitat at that time. Periodically, they would grasp the base of a willow shrub with their mouth and pull it from the ground, often shaking it. They would then chase something and crush it. After a flurry of such activity at a bush they would sit and eat. Closer inspection with a spotting scope during the "eating" phase revealed they were consuming what appeared to be lemmings. Inspection of the sites after the bears left revealed the smashed carcasses of several collared lemmings. It is possible other species were consumed, but the collared lemmings were the only remains found. Similarly, Pedersen (1962) describes polar bears capturing the "quick-moving lemmings by turning over the stones under which they were hiding." Miller and Woolridge (1983) report a female polar bear catching and eating a small rodent that they thought was likely *Microtus pennsylvanicus* in the Churchill area.

9. Capelin (*Mallotus villosus*)

Periodically, large numbers of capelin are found in schools in the near-shore waters all along the coast from Churchill to Cape Churchill and south at least to the Broad River. These events usually occur in mid to late July and on several occasions we have seen polar bears actively feeding on the fish. The bears wade in shallow rocky areas as water recedes immediately after high tide and consume mouthfuls of the fish that are trapped in shallow impoundments among the rocks. We have observed this behavior near Churchill, Watson's Point, Point Pakulak, and in the shoals east of the Canadian Wildlife Service tower at Cape Churchill (fig. 11). Dyck and Romberg (2007) observed polar bears successfully catching and eating arctic char (*Salvelinus alpinus*) and fourhorn sculpin (*Myoxocephalus quadricornis*).

FIGURE 11. One of many remnant collections of dying capelin trapped in the rocks near Churchill on 8 July 2009.

10. Northern Pike (*Esox lucius*)

On 23 June 2005 R.F.R. was in the midst of boreal forest bird inventory work at Skidmore Lake in the Center of Wapusk National Park when he observed an exceptionally fat female polar bear along the shore of the lake about 300 m north of his camp. She was standing in the flooded *C. aquatilis* that forms a 1–2 m border in the shallows along the lake. She appeared to be swatting at something and eventually grabbed it and moved on shore. Once there, she began eating the object. After she moved farther north, he walked along the shore and found the remains of a large fish and identified it definitively as a northern pike. From the size of the head, he estimated it was in the 1 m or so size range. Walking farther along the shore he found the remains of five additional such fish. He also caught several of these in the same habitat and one weighed approximately 10 kg. Skidmore Lake area is a well-known and studied polar bear denning area.

11. Lyme Grass Seed Heads (*Leymus arenarius*)

Adult male polar bears were observed foraging on the ripening seed heads of lyme grass that grows on the beach ridges adjacent to Hudson Bay on the east coast of Wapusk National Park south of the White Whale River. Individuals walked into stands of the grass, stopped and removed the seed heads with an action from the side of their mouth that appeared to use their molars and premolars. Inspection of the plants after the bear left the stand of grass revealed stems chewed to below where the seed head would have been. Gormezano and Rockwell (2013a, 2013b) reported remnants of lyme grass seeds in numerous polar bear scats. The length of foraging bouts varied, but one individual was observed foraging in this fashion for more the 15 minutes. Inspection of coastal stands of lyme grass in late July and early August often reveals plants that have been foraged on this way.